

the ORIGIN



of our
SPECIES

CHRIS STRINGER

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To the memory of lost family Tony and David, and lost colleagues Bill, Clark and Roger

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We have just celebrated the 150th anniversary of the publication of Darwin's *On the Origin of Species* and his 200th birthday, and evolution by natural selection is now widely accepted. But what do we know about the origin of our own species, *Homo sapiens*? Despite the fascinating and growing record of very ancient prehuman fossils, one topic has dominated recent scientific and popular discussion about evolution – our own origins. While it is generally agreed that Africa was the homeland of our earliest human ancestors, a fierce debate continues about whether it was also the ultimate place of origin of our own species, and of everything that we consider typical of our species, such as language, art and complex technology. Originally centred on the fossil record, the debate has grown to encompass archaeological and genetic data, and the latter have become increasingly significant, now even including DNA from Neanderthal fossils. Yet much of these new data and the discussion surrounding them are buried in highly technical presentations, scattered in specialist journals and books, so it is difficult for a general readership, however informed, to get an accessible overview. In this book I want to try and provide a comprehensive – but comprehensible – account of the origin of our species from my position in these debates over the last thirty years or so. I hope my book will make every reader think about what it means to be human, and change their perceptions about our origins – writing it has certainly changed some of mine!

I regularly give talks on human evolution and receive hundreds of enquiries on this topic every year from the media and the public. The same questions recur time and again, and in this book I will try to answer them. These questions include:

What are the big questions in the debate about our origins?

How can we define modern humans, and how can we recognize our beginnings in the fossil and archaeological record?

How can we accurately date fossils, including ones beyond the range of radiocarbon dating?

What do the genetic data really tell us about our origins, and were our origins solely in Africa?

Are modern humans a distinct species from ancient people such as the Neanderthals?

How can we recognize modern humans behaviourally, and were traits such as complex language and art unique to modern humans?

What contact did our ancestors have with people like the Neanderthals, and were we the cause of their extinction?

Do archaic features in modern human fossils and genes outside Africa indicate

hybridization?

What does DNA tell us about the Neanderthals, and possible interbreeding with modern humans?

What can we learn from a complete Neanderthal genome, and will we ever clone a Neanderthal?

What forces shaped the origins of modern humans – were they climatic, dietary, social or even volcanic?

What drove the dispersals of modern humans from Africa, and how did our species spread over the globe?

How did regional ('racial') features evolve, and how significant are they?

What was the 'Hobbit' of the island of Flores, and how was it related to us?

Has human evolution stopped, or are we still evolving?

What can we expect from future research on our origins?

It is now over twenty years since the publication of the seminal *Nature* paper 'Mitochondrial DNA and Human Evolution', by Rebecca Cann, Mark Stoneking and Allan Wilson that put modern human origins and 'Mitochondrial Eve' on the front pages of newspapers and journals all over the world for the first time. Not only did that paper focus attention on the evolution of our own species, but it also led to a fundamental reformulation of scientific arguments about the way that we look at our own origins. A year after that publication, I wrote the paper 'Genetic and Fossil Evidence for the Origin of Modern Humans' for the journal *Science* with my colleague Peter Andrews, that set out the contrasting models of modern human origins that have dominated debate ever since: Recent African Origin, and Multiregional Evolution. Later in the book we will see how these models have fared in the face of many new discoveries, but in the first chapter I will look at some of the big questions of modern human origins, including what diagnoses our species, what the recent debates are all about, and how the different models lay out expectations of what we should find in the record of modern human evolution, from fossils, archaeology and genetics.

The Big Questions

It is barely 150 years since Charles Darwin and Alfred Russell Wallace presented their ideas on evolution to the world. A year later, in 1859, Darwin was to publish one of the most famous of all books, *On the Origin of Species*. Then, the first fossil human finds were only beginning to be recognized, and palaeontology and archaeology were still in their infancy. Now, there is a rich and ever-growing record from Africa, Asia and Europe, and I have been privileged to work in one of the most exciting eras for discoveries about our origins. There have been highly significant fossil finds, of course, but there have also been remarkable scientific breakthroughs in the amount of information we can extract from those finds. In this first chapter I am going to outline the evidence that has been used to reconstruct where our species originated, and the very different views that have developed, including my own. There are in fact two origins for modern human features that we need to consider. Here, I will talk about our species in terms of the physical features we humans share today, for example, a slender skeleton compared to our more robust predecessors, a higher and rounded braincase, smaller brow ridges and a prominent chin. But there are also the characteristics that distinguish different geographic populations today – the regional or ‘racial’ characteristics, such as the more projecting nose of many Europeans, or the flatter face of most Orientals. I will discuss their quite different origins later in the book.

In *The Descent of Man* (1871), Darwin suggested that Africa was the most likely evolutionary homeland for humans because it was the continent where our closest relatives, the African apes, could be found today. However, it was to be many years before the fossil evidence that was ultimately to prove him right began to be discovered. Before then, Europe with the Neanderthals, ‘Heidelberg Man’ and the spurious ‘Piltdown Man’, and Asia with ‘Java Man’, were the foci of scientific attention concerning human ancestry. But the 1921 discovery of the Broken Hill skull in what is now Zambia, and the 1924 discovery of the Taung skull (from South Africa), started the process that gave Africa its paramount importance in the story of human evolution, even if that process still had many years to run. By the 1970s a succession of fossils had established that Africa was not only the place of origin for the human line (i.e. the continent in which the last common ancestor of humans and chimpanzees lived), but was probably also where the genus *Homo* (humans) had originated. But where did our own species, *Homo sapiens* (modern humans), originate? This was still unclear in the 1970s and remained so until quite recently.

When Charles Darwin wrote in the *Origin of Species*, ‘light would be thrown on the origin of man and his history’, he was reluctant to say any more on the subject, as he admitted

twelve years later in the introduction to *The Descent of Man*: ‘During many years I collected notes on the origin or descent of man, without any intention of publishing on the subject, but rather with the determination not to publish, as I thought that I should thus only add to the prejudices against my views.’ But in the intervening years he had been fortified by a growing number of influential supporters, and thus felt ready – finally – to tackle the controversial topic of human origins. He then went on to say: ‘the sole object of this work is to consider, firstly, whether man, like every other species, is descended from some pre-existing form; secondly, the manner of his development; and thirdly, the value of the differences between the so-called races of man’. However, Darwin acknowledged that there were still many doubters, something that unfortunately remains as true today as it was then: ‘It has often and confidently been asserted, that man’s origin can never be known: but ignorance more frequently begets confidence than does knowledge: it is those who know little, and not those who know much, who so positively assert that this or that problem will never be solved by science.’

Darwin then proceeded to pay tribute to a number of other scientists for their work on human origins, particularly the German biologist Ernst Haeckel, and this is especially interesting as Haeckel differed from him and Thomas Huxley (‘Darwin’s bulldog’) over a critical question about our origins, a question that continues to be debated even today. In *The Descent of Man* Darwin wrote: ‘We are naturally led to enquire, where was the birthplace of man at that stage of descent when our progenitors diverged from the catarrhine stock [the catarrhines group includes apes and monkeys]? ... In each great region of the world the living mammals are closely related to the extinct species of the same region. It is therefore probable that Africa was formerly inhabited by extinct apes closely allied to the gorilla and chimpanzee; and as these two species are now man’s nearest allies, it is somewhat more probable that our early progenitors lived on the African continent than elsewhere.’ However, he then proceeded to caution, ‘But it is useless to speculate on this subject ... as there has been ample time for migration on the largest scale.’

Not only did Darwin have to deal with a dearth of fossil evidence in 1871, including a complete absence of any human-like fossils from Africa, but there was also no knowledge of the concept of continental drift (the idea that landmasses have migrated in the past, splitting and realigning as they moved across the Earth’s surface). This process is now known to underlie many of the present distributions of plants and animals (for example, the unique assemblages of species found in places like Australia and New Zealand). Previously, to explain puzzling links between species in different regions, now-sunken continents were often postulated. For example, lemurs are rather primitive primates that today are found only on the island of Madagascar, some 300 miles off the coast of Africa, but ancient lemur-like fossils had been found in the Indian subcontinent, and such similarities led the British zoologist Philip Sclater to hypothesize in 1864 that there was once a large continent, which

he named Lemuria, stretching across much of what is now the Indian Ocean.

Using the concept of this lost continent, Haeckel argued for a different ancestral homeland for humans: ‘There are a number of circumstances which suggest that the primeval home of man was a continent now sunk below the surface of the Indian Ocean, which extended along the south of Asia ... towards the east; towards the west as far as Madagascar and the southeastern shores of Africa. By assuming this Lemuria to have been man’s primeval home, we greatly facilitate the explanation of the geographical distribution of the human species by migration.’ Moreover, Haeckel differed from Darwin and Huxley in favouring the gibbon and orang-utan of southeast Asia as better ape models for human ancestry than the gorilla and chimpanzee of Africa. And whereas Darwin followed the geologist Charles Lyell in arguing that the fossil record of human evolution was still unknown because the right regions had not yet been searched (in particular Africa), Haeckel preferred the explanation that most of the critical evidence was now sunk beneath the Indian Ocean.

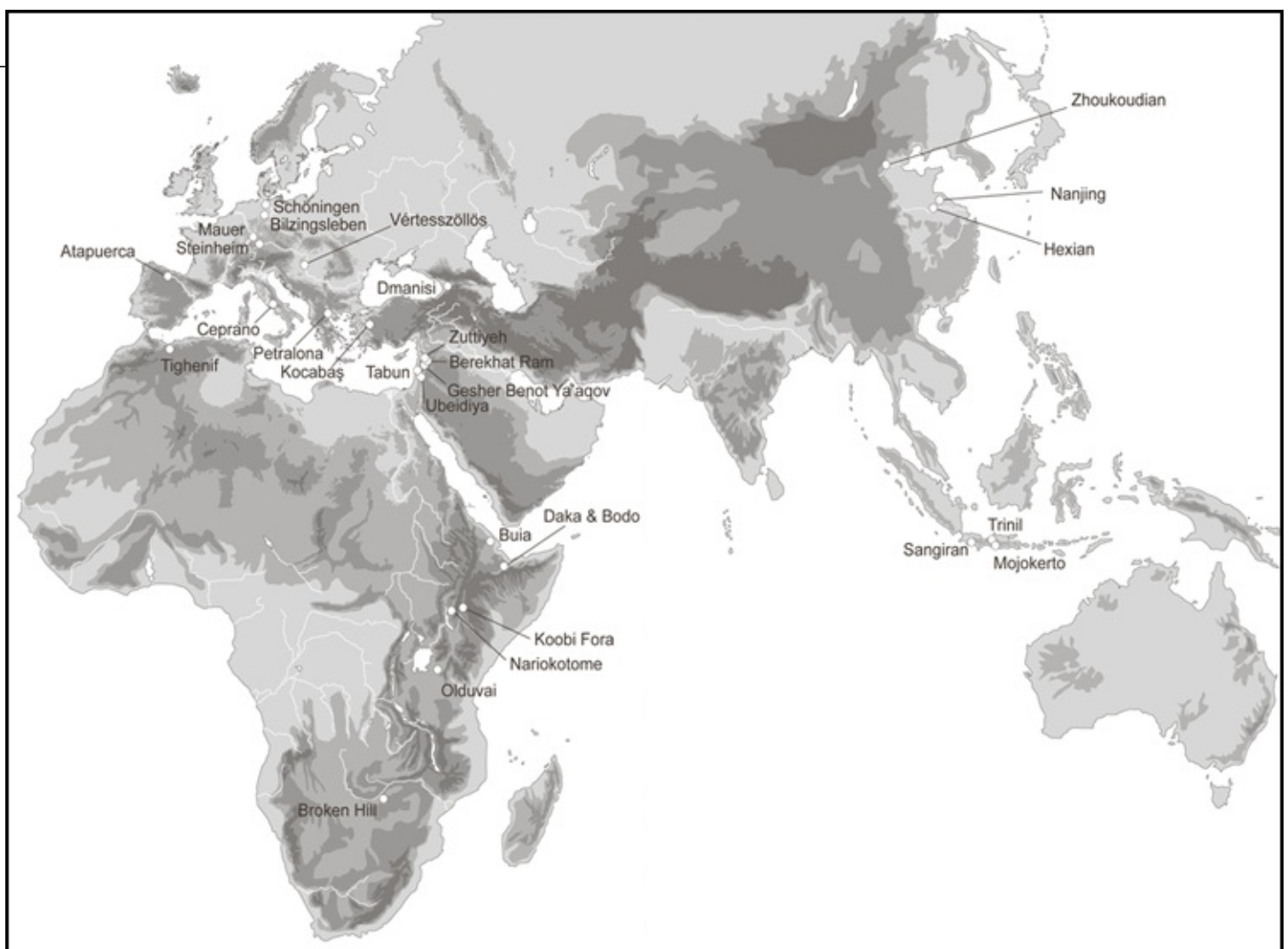


Eugène Dubois and his *Pithecanthropus erectus* skull.

During Darwin’s lifetime, the Neanderthals were already known from their fossil remains as ancient inhabitants of Europe. While some scientists pushed them into the position of ‘missing links’, reconstructing them with bent knees and grasping big toes, others like Huxley recognized them as big-brained, upright and unmistakably human. Darwin never lived to see the first discovery of a really primitive human fossil, announced by a Dutch doctor, Eugène Dubois, in 1891. Dubois had been inspired by Haeckel’s writings to get an army posting to what was then the Dutch East Indies (now Indonesia), to search for ancient remains. Haeckel had created the name *Pithecanthropus alalus* (‘Ape Man without speech’) for a hypothetical link between apes and humans that he believed had once lived in Lemuria. Dubois was

blessed with luck in his excavations on the island of Java, and soon found a fossilized and ape-like skull-cap, and a human-looking thigh bone. He named these *Pithecanthropus* (in honour of Haeckel) *erectus* (because the femur indicated this creature walked upright, as we do). We now know this species as *Homo erectus*, a wide-ranging and long-lived species of early human. But because this first find of the species was made on the Indonesian island of Java, it tended to reinforce Haeckel and Dubois's notions of a Lemurian/southern Asian origin for humans, rather than an African one.

In naming *Pithecanthropus erectus*, Dubois was following the system laid down over a century earlier by that greatest of all classifiers, the Swedish naturalist Carl Linnaeus. The Chinese sage Confucius said that it was 'a wise man' who specified the names of things, and by happy coincidence this was the name, in Latin, that Linnaeus chose for the human species *Homo sapiens*. Before Linnaeus there were many different ways of naming and grouping plants and animals, often based at random on particular features that they showed – colour, say, how they moved around, or what they ate. But Linnaeus believed in grouping living things by the bodily features they shared, and at the heart of his system were the two names applied to every natural kind, or species – its group or genus name capitalized, and its particular species name. Thus *Homo* ('Man') and *sapiens* ('wise'). The system is a bit like a surname (the genus name *Homo*) and a first name (differentiating the different children with a particular surname, in our case *sapiens*). In the most-cited tenth edition of his book *Systema Naturae* (1758) he also named four geographical subspecies: '*europaeus*', '*afri-*', '*asiaticus*' and '*americanus*', introducing some dubious anecdotal behavioural distinctions in line with then current European notions about the superiority of the European subspecies – for example, while *europaeus* was, of course, governed by laws, *americanus* was governed by customs, *asiaticus* by opinions and the African subspecies *afri-* by impulse.



Map showing early human sites.

In the early 1900s, evidence continued to accumulate in favour of a non-African origin for modern humans and the focus returned to Europe. Further Neanderthal remains were found in Croatia and France, and a more ancient and primitive fossil jawbone was unearthed in the Mauer sandpit near Heidelberg in Germany in 1907. As enough material began to accumulate, scientists started to build evolutionary trees from the fossil evidence. These tended to fall into two main categories: ones where the fossils were arranged in a linear sequence leading from the most primitive form (e.g. 'Java Man' or 'Heidelberg Man') to modern humans, with few or no side-branches (like a ladder); and others (like a bush) where there was a line leading to modern humans, and the other fossils with their primitive features were placed in an array of side-branches leading only to extinction.



A replica of the jawbone unearthed in the Mauer sandpit near Heidelberg in Germany in 1907, together with one of the Boxgrove incisor teeth.

The combination of Darwin's and Wallace's publications on the transmutation of species and a proliferating Pleistocene fossil human record led to the expectation that there must have been many more ancient species of humans (the Pleistocene is a recent geological epoch, poorly dated during Darwin's time, but now believed to stretch from about 12,000 to 2.5 million years ago). William King had named the first fossil-based species *Homo neanderthalensis* in 1864, from the skeleton discovered in the Neander Valley in 1856. Within fifty years, the new European finds were being assigned to dozens of new human species in an unfortunate tumult of typology, where trivial differences were elevated to assume real biological significance. Thus, the completely modern-looking remains that had been found in the sites of Cro-Magnon, Grimaldi, Chancelade and Oberkassel became the human species '*spelaeus*', '*grimaldii*', '*priscus*' and '*mediterraneus*', respectively, while the remains from Spy, La Moustier and La Chapelle-aux-Saints became '*spyensis*', '*transprimigenius*' and '*chapelensis*', despite their resemblance to the remains already designated *H. neanderthalensis* from the Neander Valley. This trend for what we can call extreme 'splitting' continued up to about 1950, when the pendulum swung back to the opposing tendency to 'lump' fossils together in just a few species.

Suggestions that Europe may have hosted even more primitive human relatives started to emerge from a gravel pit at Piltdown in southern England in 1912, giving rise to yet another species called *Eoanthropus dawsoni* ('Dawn Man of Dawson' – Charles Dawson being the principal discoverer). Parts of a thick but large-brained skull, coupled with a distinctly ape-like jaw, turned up there with ancient animal fossils and primitive stone tools, suggesting an age as great as that of 'Java Man'. Africa had nothing to compare with these burgeoning finds but that finally began to change in the 1920s. However, circumstances were such that these first finds still failed to switch the focus of human origins to Africa.

The Broken Hill (Kabwe) skull, discovered in 1921, was the first important human fossil from Africa, but it was a puzzling find. Although it was assigned to the new species *Homo rhodesiensis* by Sir Arthur Smith Woodward of the British Museum, the Czech-American

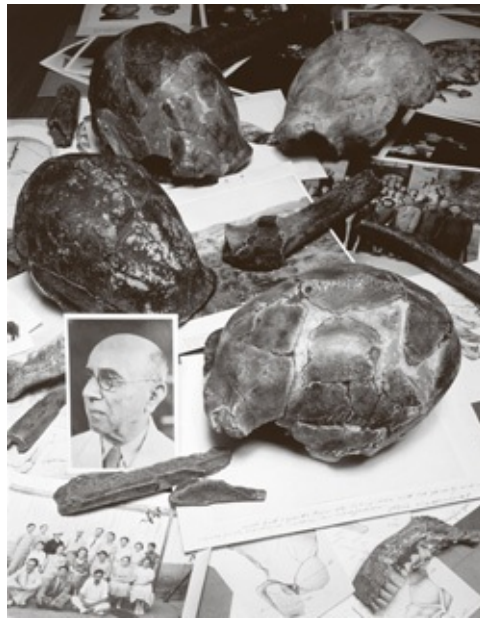
anthropologist Aleš Hrdlička dubbed it ‘a comet of man’s prehistory’ because of the difficulty in deciphering its age and affinities. The skull was found in cave deposits that were being quarried away during metal ore mining, in what is now Zambia (then the British colony of Northern Rhodesia). It’s one of the most beautifully preserved of all human fossils, but it displays a strange mixture of primitive and advanced features, and its face is dominated by an enormous brow ridge glowering over the eye sockets. And because it was found during quarrying, which eventually destroyed the whole Broken Hill mine, its age and significance remain uncertain even today (but see the final chapter for the latest developments).

Three years later an even more primitive find was made in a limestone quarry at Taung, South Africa – a skull that looked like that of a young ape. It was studied by a newly established Professor of Anatomy in Johannesburg, named Raymond Dart, and in 1925 he published a paper in the scientific journal *Nature*, making some remarkable claims about the fossil. He argued that it showed a combination of ape and human features, but that its teeth, brain shape and probable posture were human-like. Dart named it *Australopithecus africanus* (‘Southern ape of Africa’), and he declared that it was closely related to us, and even a potential human ancestor. Dart’s claims were treated with great scepticism by the scientific establishment, particularly in England. This was partly because of judgements about Dart’s youth and relative inexperience, and partly because the fossil was that of a child (young apes may look more ‘human’ than adult apes). Others thought that the finds from Java, Heidelberg and Piltdown provided much more plausible ancestors than *Australopithecus africanus*. And finally, the location and estimated age of Taung also counted against it.

No one (not even Darwin and Huxley) had considered southern Africa as a location for early human evolution, and as it was guessed to be only about 500,000 years old, it was thought too recent to be a genuine human ancestor. Instead, it was considered to represent a peculiar kind of ape, paralleling humans in some ways. We now know, of course, that the australopithecines represented a long and important phase of human evolution that lasted for over 2 million years, and which is recognized at sites stretching from Chad in the Sahara to many more in South Africa. And we have also known since their exposure in 1953, that the misleading Piltdown remains were fraudulent, and nothing to do with our ancient ancestry.

Other finds made at this time continued to keep the focus outside of Africa, and those made in cave deposits at Zhoukoudian near Beijing from 1921 onwards began to reveal a Chinese counterpart to Java Man initially dubbed *Sinanthropus pekinensis* (‘Chinese Man of Peking’). Systematic excavations carried out from 1927 until the present day have yielded many skull and body parts of humans who lived there about half a million years ago, people who resembled the growing collection of fossils from Java closely enough for them to be eventually grouped together in the single species *Homo erectus*. This species is a crucial one for studies of our origins, because it’s at the heart of radically different views of our evolution that have emerged over the last seventy years or so. Most anthropologists

recognize the existence of at least two human species during the last million years – the extinct *Homo erectus* and our own species, *Homo sapiens* – but there are very different views on how these species are related.

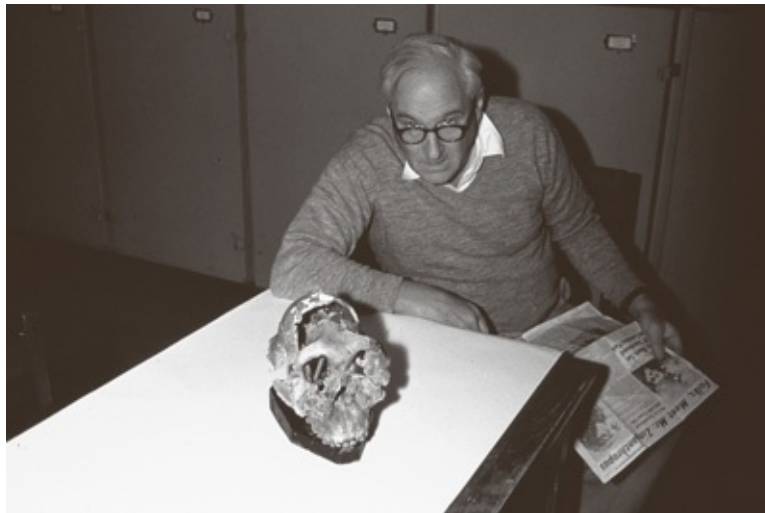


Franz Weidenreich and some of the 'Peking Man' fossils of *Homo erectus* that inspired him to create an early version of the Multiregional model of human origins.

What is now known as the multiregional model of modern human origins was first proposed in the 1930s by Franz Weidenreich, a German anthropologist, who based many of his arguments on studies of the Zhoukoudian *Homo erectus* fossils. Weidenreich suggested that *Homo erectus* gave rise to *Homo sapiens* across its whole range which, about 1 million years ago, included Africa, China, Indonesia and perhaps Europe. In his view, as the species dispersed around the Old World (it's not known from regions such as Australia and the Americas), it developed the regional variation that lies at the roots of modern 'racial' differentiation. Particular features in a given region persisted in the local descendant populations of today. For example, he argued from the fossils that Chinese *Homo erectus* specimens had the same flat faces and prominent cheekbones as modern Oriental populations while Javanese *Homo erectus* had robustly built cheekbones and faces that jutted out from the braincase, characteristics argued to be especially marked in modern Australian Aborigines.

At the other extreme from Weidenreich's multiregional model was the view that the special features of modern humans (such as a high forehead, a chin and a slender skeleton) would have required a long time to evolve, and hence the line leading to *Homo sapiens* (the 'pre-sapiens' lineage) must have been very ancient, and developed in parallel with large-browed and robust forms such as *Homo erectus* and the Neanderthals. This is an old idea, which came to prominence early in the twentieth century through influential researchers like Marcellin Boule (France) and Arthur Keith (United Kingdom), and aspects of it were taken up later by Louis Leakey, working in Kenya and Tanzania. The supporting evidence came and

went through the last century, including at times specimens like Piltdown and the modern-looking Galley Hill skeleton from Kent – the former now known to be a fake, and the latter wrongly dated.



Louis Leakey with the Olduvai Gorge '*Zinjanthropus*' skull, which his wife Mary discovered in 1959. It was the first important fossil to be dated by the Potassium-Argon method.

Between the extremes of multiregionalism (which potentially included every human fossil in our ancestry) and the pre-*sapiens* model (which excluded most of them), there were intermediate models, ones which featured early Neanderthals in the story. The critical fossils at this time were from Mount Carmel in what was then Palestine. They were discovered by an international expedition excavating a series of caves near Haifa during the late 1920s and 1930s. In two of the caves, Skhul and Tabun, they found human fossils that had apparently been intentionally buried. Moreover, they were associated with the kinds of stone tools that in Europe were associated with the Neanderthals. And yet the fossils seemed to show mixtures of Neanderthal and modern characteristics, so how should they be interpreted? In the 1930s there were no accurate methods of dating available, and so the Tabun and Skhul fossils were assumed by their describers Theodore McCown and Arthur Keith to be roughly contemporaneous with each other. Some suggested that the finds might represent hybrids between moderns and Neanderthals, but McCown and Keith preferred to regard them as members of a single but variable ancient population, perhaps one close to the divergence of the Neanderthal and modern lines (in fact Keith could not quite abandon his pre-*sapiens* leanings and thought that they were still probably off the line leading to us, because of their Neanderthal features).

But others saw them as evidence for a pre-Neanderthal rather than pre-*sapiens* ancestry for modern humans, with the late or 'classic' Neanderthals subsequently heading off the main line to the sidings of extinction. Following this line of argument, American palaeoanthropologist F. Clark Howell developed a neat scenario during the 1950s where 'unspecialized Neanderthals' about 100,000 years ago became isolated in Europe by the last Ice Age, and

evolved away from *Homo sapiens*. At the same time, those in the Middle East (such as Tabun) evolved towards modern humans via forms like those found at Skhul. Then, to complete the story, about 35,000 years ago these Middle Eastern ‘proto Cro-Magnons’ migrated into Europe and replaced their European Neanderthal cousins.

In contrast to this ‘early Neanderthal’ model of modern human origins, which gave the Neanderthals at least a bit part in our evolution, there were two developments out of Weidenreich’s multiregionalism after his death in 1948 that returned the Neanderthals to a central role in our evolution, and in one case even extended their role globally. American anthropologist Carleton Coon used new fossil material to develop a comprehensive global scheme of the evolution of five different lineages of *Homo erectus*, two in Africa, and one each in Europe, China and Australia. These five lineages evolved largely independently to become what Coon regarded as the modern races of *Homo sapiens*: ‘Capoid’ (the Bushman of South Africa and related peoples), ‘Negroid’, ‘Caucasoid’, ‘Mongoloid’ and ‘Australoid’.

In this respect, Coon differed fundamentally from his mentor, since Weidenreich considered human evolution to consist of a network of lineages constantly exchanging genes and ideas, whereas Coon was quite frank about the divided lineages and the implications of their inferred different rates of evolution: ‘Wherever *Homo* arose, and Africa is at present the most likely continent, he soon dispersed, in a very primitive form, throughout the warm regions of the Old World ... If Africa was the cradle of mankind, it was only an indifferent kindergarten. Europe and Asia were our principal schools.’

The American palaeoanthropologist C. Loring Brace gave Weidenreich’s ideas a distinctly Neanderthal twist by arguing that *Homo erectus* evolved to modern humans in each part of the populated world by passing through a ‘neanderthaloid’ phase. In essence, according to Brace, the Neanderthals and equivalent ancient people across the inhabited world used their front teeth as tools for manipulating food and materials, and this is what produced their especially prominent midfaces, large incisor teeth and distinctive skull shape. When more advanced tools of the Upper Palaeolithic (Upper Old Stone Age) were invented about 35,000 years ago, demands on the teeth and jaws were lifted, and so the face and skull were transformed into the shape we have today.

These were the main ideas about the origin of modern humans that I set out to test when began my studies for a Ph.D. at Bristol University in 1970: the global multiregional model and its Braceian development, the early Neanderthal model, the pre-*sapiens* model (with no place for *erectus* or Neanderthals), and one rather vaguer scheme developed by anthropologists Bernard Campbell and Joseph Weiner called the ‘spectrum hypothesis’. This argued that ancient humans had different blends of what would become modern human characteristics, and they contributed in part, and differentially, to the evolution of *Homo sapiens*. So in a sense the spectrum hypothesis was multiregional, but some lineages had a much greater contribution to our ancestry than others. A bit of a revolution was underway

around 1970, as computing power started to increase and began to impact the biological sciences. Most analyses of human evolution up to 1970 were based on direct observation and where measurements of a fossil were taken, these were usually compared individually or through an index of just two measurements. However, multivariate programmes were becoming available that could look at large numbers of measurements and specimens simultaneously, allowing more sophisticated studies of differences in size and shape. Such analyses were at the centre of my studies for a doctorate, and in July 1971 I left the UK on a trip to museums and research institutes in ten European countries. The aim was to gather as many data as possible on the Neanderthals and their modern-looking successors in Europe, the Cro-Magnons, to see whether the evolutionary pattern was one of continuity or rupture. I only had a modest grant from the Medical Research Council for a four-month trip, and so I drove my old car, sleeping in it, camping or staying in youth hostels – in Belgium I even spent one night in a shelter for the homeless. I survived many adventures, including several border confrontations and two robberies, but by the end of my 5,000-mile trip I had collected one of the largest data sets of Neanderthal and early modern skull measurements assembled by anyone up to that time.

Over the next two years I analysed this information, adding comparative data on non-European fossils and modern human populations (the latter generously supplied by the American anthropologist William Howells). The measurements were transferred to data cards and fed into a computer the size of several rooms, but which had less processing power than my last mobile phone! Nevertheless, the results were instructive. Neanderthal skulls were not more similar to those of recent Europeans than they were to Africans, Eskimo or Native Tasmanians, and Cro-Magnon skulls did not neatly slot between the Neanderthals and recent Europeans. Early modern skulls from around the world seemed to cluster with their modern counterparts rather than with any archaic skulls from the same regions. The former results provided no support for a Neanderthal ancestry for the Cro-Magnons, and the latter results contradicted multiregional and spectrum expectations. Studying the sequence in Europe before Neanderthal times also gave no support to the pre-*sapiens* model either, because very early European fossils could not be divided into modern-like and Neanderthal-like – they seemed to show the gradual development of only Neanderthal features through time.

Things were not quite as clear in the Middle East, although there did not seem to be any ‘intermediate’ fossils between Neanderthals and moderns there either. Skulls from Tabun and the Israeli cave of Amud seemed to be basically Neanderthal, while those from Skhul Cave seemed much more modern. But because none of these finds were well dated in the 1970s, I couldn’t exclude the possibility that, given enough time, the Israeli Neanderthals could have been transformed into early moderns, in line with the early Neanderthal model of scientists like Clark Howell. However, a surprising alternative ancestor for the Skhul and Cro-Magnon early moderns did emerge from my results. A skull discovered in 1967 in the Omo Kibish

region of Ethiopia, by a team led by Richard Leakey (the son of the famous prehistorians Louis and Mary Leakey), looked very modern in my skull shape analyses, confirming the first studies by anatomist Michael Day – and yet preliminary dating work suggested it could have been as much as 130,000 years old, more ancient than most Neanderthals. And there was an enigmatic North African skull, found in the Moroccan site of Jebel Irhoud in 1961. In skull shape it seemed Neanderthal in some ways, yet its facial shape was non-Neanderthal, partly primitive and partly modern. With an age thought to be only around 40,000 years it was difficult to fit Jebel Irhoud into any scenario, but it and the Omo skull provided clues that Africa was going to have its own story to tell, when more data came in.

As my work developed through the 1970s and early 1980s, I gravitated increasingly towards what Bill Howells in 1976 had dubbed the ‘Garden of Eden’ or ‘Noah’s Ark’ model. This was named not because Howells was any kind of biblical creationist, but because of the implication that all modern human variation had developed from a single centre of origin. A lack of fossils from many parts of the world, together with inadequate dating for many of those we did have, meant that neither Howells nor I could specify where that centre of origin might have been, although we thought we could exclude the European and Middle Eastern territories of the Neanderthals. We both felt that the distinctive shared features of modern humans such as the high rounded skull, small brows and chin, implied a recent common origin, as otherwise there would have been much greater differentiation over time. And I started to move away from the then widespread idea that fossils as different-looking as Broken Hill, the Neanderthals and Cro-Magnon should all be classified with us as variants of our species, *Homo sapiens*. Initially I agreed with some other workers in differentiating ‘anatomically modern *sapiens*’ (such as Skhul and Cro-Magnon) from ‘archaic *sapiens*’ forms such as Neanderthals and Broken Hill. But during the 1980s, I increasingly favoured limiting the *sapiens* term to fossils closely resembling us. Moreover, along with a few other heretics, started to argue that the Neanderthals should be returned to the status granted them by William King in 1864 as a distinct species, *Homo neanderthalensis*. I also suggested that the Broken Hill skull found in 1921 could be grouped with more primitive European forms (for example the Heidelberg jaw discovery of 1907) as *Homo heidelbergensis*.

As my views on our origins were developing towards a single-origin model, evidence began to accumulate that Africa was especially important in this story. The Omo Kibish find was joined by material from the sites of Border Cave and Klasies River Mouth Caves in South Africa. Moreover, new dating work hinted that Africa was not the backwater in cultural evolution that most considered it to be. Archaeologists such as Desmond Clark and Peter Beaumont argued that it might instead have been leading the way in the sophistication of its stone tools. By 1980 I was privately convinced that Africa was the main centre of our evolution but, because of dating uncertainties, I could not rule out the Far East as also playing a role. It took another four years for me to take a strong ‘Out of Africa’ stance

publicly, as various lines of evidence started to fit together in my mind. However, further confusion was sown by the strong re-emergence of Weidenreich's multiregional views in 1984. These were given a new lease of life by Milford Wolpoff (USA), Alan Thorne (Australia) and Wu Xin-zhi (China). They distanced themselves from Coon's views by returning to Weidenreich's emphasis on the importance of gene flow between the geographic lines, considering the continuity in time and space between the various forms of *Homo erectus* and their regional descendants to be so complete that all of them should be classified with modern people as representing only one species – *Homo sapiens*. Thus in this model there was no real 'origin' for the modern form of *Homo sapiens*. A feature like the chin might have evolved in a region such as Africa, and spread from there by interbreeding across the human range, followed by selection for it if it was an advantageous characteristic. Another feature like our high forehead might have developed in, say, China, and then similarly spread from there through interbreeding. Thus modern humans could have inherited their 'local' features through continuity with their ancient predecessors, while global characteristics were acquired via a network of interbreeding.



Milford Wolpoff, an architect of Multiregionalism, with a *Homo erectus* skull from Java.

But new developments in genetics research were about to have a huge impact. In 1982, I became aware of research work on a peculiar type of DNA that is found outside the nucleus of cells, in the mitochondria. These are little bodies that provide the energy for each cell, bodies that probably originated from a once-separate bacterium, which somehow survived being engulfed by a primitive cell. They then co-evolved to confer mutual advantage, and developed into the mitochondria that most organisms have throughout their cells. In humans the DNA of a mother's mitochondria is cloned in her egg when it becomes the first cell of her child, and little or no mitochondrial DNA from the father's sperm seems to be incorporated at fertilization. This means that mitochondrial DNA (mtDNA) essentially tracks evolution through females only (mothers to daughters), since a son's mtDNA will not be passed on to his children. This type of DNA mutates at a much faster rate than normal (nuclear) DNA, as we will discuss later, allowing the study of short-term evolution. Early work on human

mitochondria seemed promising, showing that our species apparently had low diversity and recent origin, but the geographical patterns seemed unclear as to where that origin might be. By 1986, I had heard through the grapevine that startling new mtDNA results were on the way to publication and a year later they appeared in the science journal *Nature*, shaking up arguments about recent human evolution in such a way that things would never be the same again. This seminal publication by Rebecca Cann, Mark Stoneking and Allan Wilson put modern human origins on the front pages of newspapers, journals and magazines for the first time.

About 150 types of mtDNA from around the world were investigated, and their variation determined. Then a computer programme was used to connect all the present-day types in an evolutionary tree, with the most economical pattern of evolutionary change (mutations), reconstructing hypothetical ancestors for the living types. In turn, the programme connected those ancestors to each other, until a single hypothetical ancestor for all the modern types was created. The distribution of the ancestors implied that the single common ancestor must have lived in Africa, and the number of mutations that had accumulated from the time of the common ancestor suggested that this evolutionary process had taken about 200,000 years. This, then, was the birth of the now-famous 'mitochondrial Eve' or 'lucky mother', since the common mitochondrial ancestor must necessarily have been a female. These results seemed to provide strong evidence for a Recent African Origin view for modern humans, since the research suggested that a relatively recent expansion from Africa had occurred, replacing any ancient populations living elsewhere, along with their mtDNA lineages. However, the work was soon heavily criticized. It was shown that the kind of computer programme used could actually produce many thousands of trees which were all more or less as economical as the published one, and not all of these alternative trees were rooted in Africa. Moreover, other researchers criticized the calibration of the time when 'Eve' lived, while yet others questioned the constitution of the modern samples analysed (for example, many of the 'African' samples were actually from African-Americans). As a result, multiregionalists were, for a while at least, able to reject these mtDNA results as irrelevant or misleading, arguing that fossil evidence (and their interpretation of it) remained the only valid approach to reconstructing recent human evolution.

However, the results strongly supported the Recent African Origin view that people like Gunter Bräuer (from Hamburg) and I had been developing from the fossils. Gunter was less inclined to view *Homo sapiens* as a newly evolved species, and more inclined to think that hybridization had occurred with people like the Neanderthals, following the dispersal from Africa, but we both welcomed the new mtDNA data. For me, it gave greater confidence that even where the fossil evidence was patchier or more ambiguous, such as the Far East and Australasia, the story of replacement that I had read from the European record probably applied there too.

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